Contrasting effects of nitrogen addition on litter decomposition in forests and grasslands in China

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Abstract: Nitrogen (N) addition has profound impacts on litter-mediated nutrient cycling. Numerous studies have reported different effects of N addition on litter decomposition, exhibiting positive, negative, or neutral effects. Previous meta-analysis of litter decomposition under N addition was mainly based on a small number of samples to allow comparisons among ecosystem types. This study presents the results of a meta-analysis incorporating data from 53 published studies (including 617 observations) across forests, grasslands, wetlands, and croplands in China, to investigate how environmental and experimental factors impact the effects of N addition on litter decomposition. Averaged across all of the studies, N addition significantly slows litter decomposition by 7.02%. Considering ecosystem types, N addition significantly accelerates litter decomposition by 3.70% and 11.22% in grasslands and wetlands, respectively, clearly inhibits litter decomposition by 14.53% in forests, and has no significant effects on litter decomposition in croplands. Regarding the accelerated litter decomposition rate in grasslands due to N addition, litter decomposition rate increases slightly with increasing rates of N addition. However, N addition slows litter decomposition in forests, but litter decomposition is at a significantly increasing rate with increasing amounts of N addition. The responses of litter decomposition to N addition are also influenced by the forms of N addition, experiential duration of N addition, humidity index, litter quality, and soil pH. In summary, N addition alters litter decomposition rate, but the direction and magnitude of the response are affected by the forms of N addition, the rate of N addition, ambient N deposition, experimental duration, and climate factors. Our study highlights the contrasting effects of N addition on litter decomposition in forests and grasslands. This finding could be used in biogeochemical models to better evaluate ecosystem carbon cycling under increasing N deposition due to the differential responses of litter decomposition to N addition rates and ecosystem types.

Keywords: litter decomposition rate; N addition; ambient N deposition; litter quality; meta-analysis; forests; grasslands

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1 Introduction

Litter decomposition is acknowledged to be an important ecological process that affects soil carbon (C) and nutrient cycling and forms the basis of soil fertility maintenance (Parton et al., 2007). Previous studies have found that litter decomposition is regulated by soil and climate conditions (Bradford et al., 2014), litter quality (Manzoni et al., 2010; See et al., 2019), ambient nitrogen (N) deposition, and inputs of external N (Knorr et al., 2005; Zhang et al., 2018). These factors usually interact with each other in affecting litter decomposition. A comprehensive understanding of litter decomposition rate and its regulatory factors are essential to assess global C and nutrient budgets.

The application of fertilizer, rapid urbanization, and the development of livestock cultivation have led to annual increases in N deposition rates from regional to global scales (Lamarque et al., 2005; Liu et al., 2013). Increases in N deposition have been shown to significantly influence litter quality and the availability of soil nutrients (Hou et al., 2020). These changes have profound effects on litter decomposition rate, and have been shown in forests (Hobbie, 2008; Zhang et al., 2016), grasslands (Alster et al., 2013), wetlands (Song et al., 2018), and croplands (Zhou et al., 2018). However, the detailed results of increasing N deposition are highly inconsistent. For example, N addition significantly increased (Schuster, 2015), decreased (Freedman et al., 2016), or even showed no detectable effect on litter decomposition rate (Zhang et al., 2018) in particular circumstances. The variations in these results may be due to differences in ecosystem type, the rates of N addition, and litter quality.

Results from a previous meta-analysis indicated that the rate of N addition affected the magnitude and direction of changes in litter decomposition rate (Knorr et al., 2005). For example, low or high levels of N addition significantly inhibited litter decomposition rate, while moderate levels of N addition significantly accelerated it. However, another study reported that low levels of N addition (<6 g N/(m^2•a)) significantly stimulated litter decomposition, while moderate (6–12 g N/(m^2•a)) or high (>12 g N/(m^2•a)) levels of N addition clearly inhibited litter decomposition (Chen et al., 2015). To our knowledge, there are still very few studies which have quantified and predicted litter decomposition rate in response to N addition. Owing to the complexity and spatial heterogeneity of ecological interactions, it is difficult for any individual study to effectively resolve these differences; a general examination of the tendencies and patterns of the effects of N addition on litter decomposition would be a useful exercise.

At least two previous meta-analytical studies have been performed to evaluate the general effect of N addition on litter decomposition (Knorr et al., 2005; Zhang et al., 2018). Specifically, Knorr et al. (2005) selected 24 studies solely from North America and Europe before 2000 taken as a whole, but their sample size was insufficient to consider the impacts of the rate of N addition on litter decomposition in different ecosystem types. Zhang et al. (2018) also investigated the impacts of N addition on litter C cycling and nutrient release. Unfortunately, these studies are limited by their sample sizes. Knorr et al. (2005) attempted to assess how the various factors (differences in ecosystem types, climatic factors, the rates and forms of N addition, and ambient N deposition) interact with N addition to affect litter decomposition. In addition, some studies found that N addition had different effects on litter decomposition in the various stages of decomposition (Hobbie et al., 2012; Johansson et al., 2012; Zhang and Wang, 2012; Zhang et al., 2014). For example, N addition could promote litter decomposition in the initial stages but reduce it in the latter stages, indicating that the timing of litter decomposition rate determination was also a key factor influencing the results of an investigation. The different hypotheses generated by these studies may be due to the differences in the ecosystem types, the rates of N addition, the forms of N addition, the duration of N application, the amount of ambient N deposition, and the variables of soil and climate (Knorr et al., 2005; Aerts, 2006; Dong et al., 2020). The interactions between N addition and these factors as well as their effects on litter decomposition rate still merit additional study, since this subject is of great significance in accurately predicting the future impact of global climate change on litter decomposition.

During the previous three decades, China has experienced significant N deposition (Liu et al., 2013). A large number of field experiments, including studies on forests (Mo et al., 2006; Fang et

al., 2007), grasslands (Liu et al., 2010), wetlands (Song et al., 2011), and croplands (Zhou et al., 2018), have been performed to investigate the responses of litter decomposition to N addition. These ecosystems provide ideal situations in which to evaluate how environmental and experimental factors interact with N addition to affect litter decomposition. Therefore, a detailed comprehensive study of these responses, and the patterns and factors driving litter decomposition in response to N addition should be needed across the various habitats in China. To address the gaps in our knowledge, we performed a comprehensive meta-analysis using data from N addition experiments in the field, incorporating 617 observations drawn from 53 published studies. The effects of ambient N deposition, the rates of N addition, litter quality, and climate change on litter decomposition rate in response to N addition were examined using regression analysis.

2 Materials and methods

2.1 Data collection

Data for use in the meta-analysis were collated from peer-reviewed publications obtained from 2000 to 2020 through the Web of Science (http://webofscience.com) and the China National Knowledge Infrastructure (https://www.cnki.net/). Keyword searches such as "either N addition, N enrichment, N fertilization, N application, N input, or N deposition" and "either litter decomposition or litter mass loss" were used.

The following criteria were used to identify primary articles suitable for inclusion in the analysis: (1) the data on N addition experiments were collected only in the field; (2) the abiotic and biological conditions of the control and experimental N addition treatments were the same; (3) litter decomposition rate was reported, and mean values, standard errors, and sample sizes could be extracted from the articles; (4) values for the control and experimental N addition treatments could be separated from other experimental variables, such as the addition of phosphorus (P) compounds and N/P mixtures; and (5) multiple measurements at different time periods could be considered as independent observations.

Fifty-three articles, including a total of 617 observations, were finally selected for our study. To examine the effects of ecosystem types, N fertilizer treatments, and experimental duration on litter decomposition under N addition, we first categorized ecosystem types according to the environment and the dominant plant community (i.e., forests, grasslands, wetlands, and croplands). Then, we also categorized the forms of N addition: (1) $CO(NH_2)_2$; (2) NH_4NO_3; (3) NH_4^+; (4) NO_3^-; and (5) mixed N, such as $CO(NH_2)_2$ and glycine mixtures. Low, moderate, and high rates of N addition were defined as <5, 5–15, and ≥15 g N/(m^2•a), respectively. We further classified the data according to experimental duration (<6, 6–12, 13–24, and >24 months) in which litter decomposition was measured, ambient N deposition (<1, 1–2, 2–3, and >3 g N/(m^2•a)), the ratio of the rate of N addition to ambient N deposition (≤1, 1–5, 5–10, and >10), soil pH (<7 and ≥7), and humidity index (HI; ≤30, 30–60, and >60). HI was calculated as: HI=MAP/(AMT+10), where AMT is annual mean temperature (°C) and MAP is mean annual precipitation (mm) (Deng et al., 2019).

The environmental variables, such as ambient N deposition, the rate of N addition, AMT, MAP, and geographical locations were recorded from the selected studies. The original data were extracted directly from tables in the publications or by digitizing published graphs using the GetData Graph Digitizer (http://www.getdata-graph-digitizer.com).

2.2 Meta-analysis

A logarithmic response ratio (lnRR) was used to estimate the effect of N addition on litter decomposition rate; it was estimated using the following equation:

$$\ln \mathrm{RR} = \ln\left(\frac{x_t}{x_c}\right), \quad (1)$$

where x_t is the mean K (slope) value of litter decomposition rate resulting from the N fertilizer treatment group; and x_c is the mean K value of the control group.

The variance (v) was calculated using the following equation:

$$v = \frac{1}{n_t} \times \left(\frac{S_t}{x_t}\right) + \frac{1}{n_c} \times \left(\frac{S_c}{x_c}\right), \tag{2}$$

where n_t and n_c are the sample replications of treatment and control groups, respectively; and S_t and S_c are the standard deviations of treatment and control groups, respectively.

Standard deviation (SD) was calculated using the standard error (SE):

$$\mathrm{SD} = \sqrt{n} \times \mathrm{SE}, \tag{3}$$

where n is the sample replications of treatment or control groups.

Weighting factor (w_f) for each lnRR is:

$$w_f = \frac{1}{v}. \tag{4}$$

It should be noted that some articles did not include data on the variance and weighting by sample size, such as Peng et al. (2016), Mao et al. (2020), Sha et al. (2020), etc.

Weighted size effect (lnRR') was obtained using the following equation:

$$\ln \mathrm{RR}' = w \times \ln \mathrm{RR}, \tag{5}$$

where w is final weighting factor.

Finally, mean variance-weighted size effect was calculated as follows:

$$\ln \mathrm{RR}_{++} = \frac{\sum \ln \mathrm{RR}'_i}{\sum w_i}, \tag{6}$$

$$95\%\ \mathrm{CI} = \mathrm{RR}_{++} \pm 1.96 \times \mathrm{SE}\left(\mathrm{RR}_{++}\right), \tag{7}$$

$$\mathrm{SE}\left(\mathrm{RR}_{++}\right) = \sqrt{\frac{1}{\sum_{i=1}^{m} \sum_{j=1}^{ki} W_{ij}}}, \tag{8}$$

where $\ln\mathrm{RR}_{++}$ is weighted size effect; CI is confidence interval; W_{ij} is weighting factor; and $\ln\mathrm{RR}'_i$ and w_i are lnRR' and w of the i^{th} observation, respectively.

Weighted lnRR and 95% CI were reported as a percentage difference compared with the controls, and were calculated as follows. Mean lnRR of each group was calculated using a categorical random-effect model and CIs for the effect-size estimates were calculated using a bootstrapping procedure with 4999 iterations. All the calculations were performed using MetaWin 2.0 or 2.1 (Mao et al., 2020; Sha et al., 2020). The effects of N addition on litter decomposition rate were considered as significant when 95% CIs did not overlap with zero, and were significantly different from each other when 95% CIs of each categorical group did not overlap.

The percentage change (%change) was estimated using Equation 9:

$$\%\mathrm{change} = (\mathrm{e}^{\ln \mathrm{RR}_{++}} - 1) \times 100\%. \tag{9}$$

A positive percentage change compared with the control group indicates that N addition increases litter decomposition, while a negative change indicates that litter decomposition rate decreases compared with the control group.

2.3 Statistical analysis

To clarify the factors influencing the effects of N addition on litter decomposition rate, we used HI as an indicator of general climatic conditions, and grouped HI values into low, medium, and high categories (0–30, 30–60, and >60, respectively) following Deng et al. (2019). General linear regressions were used to evaluate the relationships between the lnRR of litter decomposition rate and the factors affecting the rate of N addition, ambient N deposition, litter quality, the ratio of the rate of N addition to ambient N deposition, AMT, MAP, and HI. All analyses were performed using SPSS 23.0 for Windows (IBM, Inc., Armonk, NY, USA), and the graphs were drawn using Origin version 9.0 (OriginLab, Northampton, MA, USA).

3 Results

As shown in Figure 1, N addition significantly affected litter decomposition, ranging from inhibition to stimulation (Fig. 1). The linear regression analysis indicated that there was a significant positive correlation of litter decomposition rate between the control group and the treatment group, with K (slope)=0.79 (P<0.001). The results suggested that N addition generally inhibited litter decomposition.

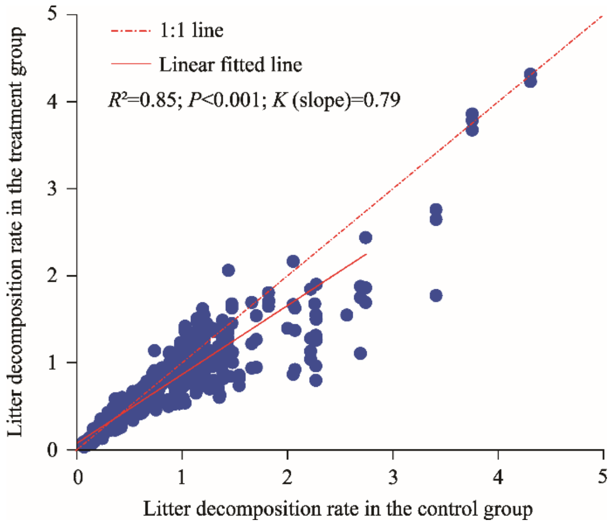

Fig. 1 Relationship between litter decomposition rate in the control group and litter decomposition rate in the treatment group. The 1:1 line represents a similar litter decomposition rate in the control group and treatment group, whereas the circle above or below this line indicates an increase or decrease in litter decomposition rate as a result of N addition, respectively.

Averaging over all of the data, N addition significantly inhibited litter decomposition rate, causing a decrease of 7.02% (Fig. 2) although the effect differed between different ecosystem types. Compared with other ecosystems, N addition significantly promoted litter decomposition in wetlands and grasslands while inhibited litter decomposition in forests, but had no effect in croplands. Litter decomposition rate response to N addition in different ecosystem types is shown in Figure 2. In addition, the rate of N addition influenced the magnitude of litter decomposition rate. When the rate of N addition was less than 5 g N/(m^2•a) in forests, litter decomposition rate was inhibited to a small but noticeable degree (–5.59%). When the rate of N addition was larger than 15 g N/(m^2•a), litter decomposition rate was significantly inhibited (–29.20%). N addition generally stimulated litter decomposition in grasslands, but the increments increased only slightly with increasing rates of N addition (Fig. 2).

The magnitude and direction of litter decomposition rate changes in response to N addition in the field could be affected by the forms of N addition and the amount of ambient N deposition (Fig. 3). Different fertilizer types had significantly different effects on litter decomposition rate. Adding mixtures of different sources of N significantly increased litter decomposition (17.93%). Specifically, $CO(NH_2)_2$ alone did not significantly affect litter decomposition rate, while other forms of N addition significantly reduced litter decomposition rate, ranging from –20.56% to –4.57%. Adding N fertilizer significantly decreased litter decomposition rates by 8.25%–21.51% for sites where the rates of N addition were 0.25-fold–10-fold greater than those of ambient N deposition (Fig. 3). When the amount of N addition was 10-fold greater than the ambient N deposition level, litter decomposition rate increased significantly by 10.45%. In the sites with low ambient N deposition (<2 g N/(m^2•a)), N addition significantly increased litter decomposition rate by approximately 2.89%–5.86%. At higher levels of ambient N deposition (≥3 g N/(m^2•a)), N addition inhibited litter decomposition rate. Experimental duration of litter decomposition, soil pH, and HI

regulated the magnitude and direction of litter decomposition rate in response to N addition (Fig. 3). Litter decomposition measured over less than 6 months increased significantly by 7.68%, while it measured over a period of 6–12 months was more obviously inhibited by 17.10%, and no significant effect was found over a 12-month monitoring period. Soil pH also influenced the effects of N addition on litter decomposition. N addition significantly inhibited litter decomposition rate in acidic soils, but caused no significant effect on litter decomposition in neutral or alkaline soils, with only a slight increase of 1.20%. HI also significantly affected the response of litter decomposition to N addition, but there were no significant differences among the treatment groups.

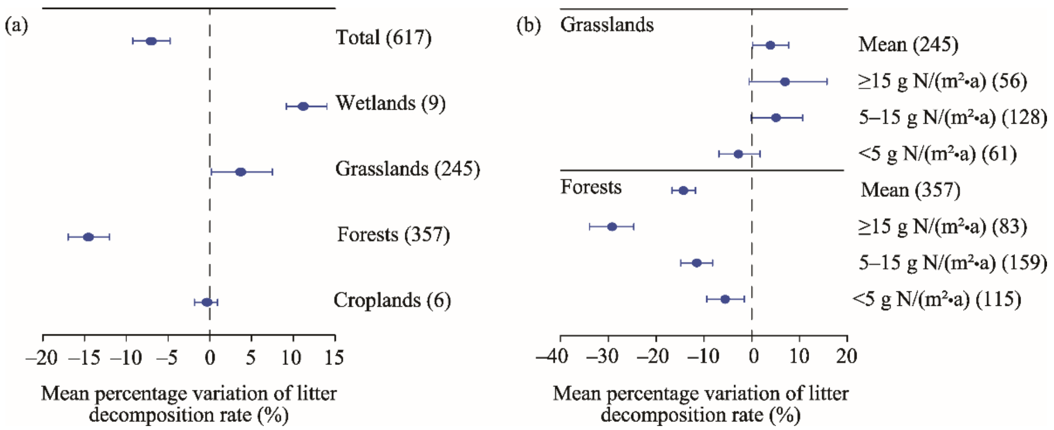

Fig. 2 Mean percentage variation of litter decomposition rates with N addition in different ecosystem types (a) and the effect of the rate of N addition on litter decomposition rate in forests and grasslands (b). The effects of N addition on litter decomposition rate were considered as significant when 95% confidence intervals did not overlap with zero, and were significantly different from each other when 95% confidence intervals of each categorical group did not overlap. Values in the brackets represent the number of observations.

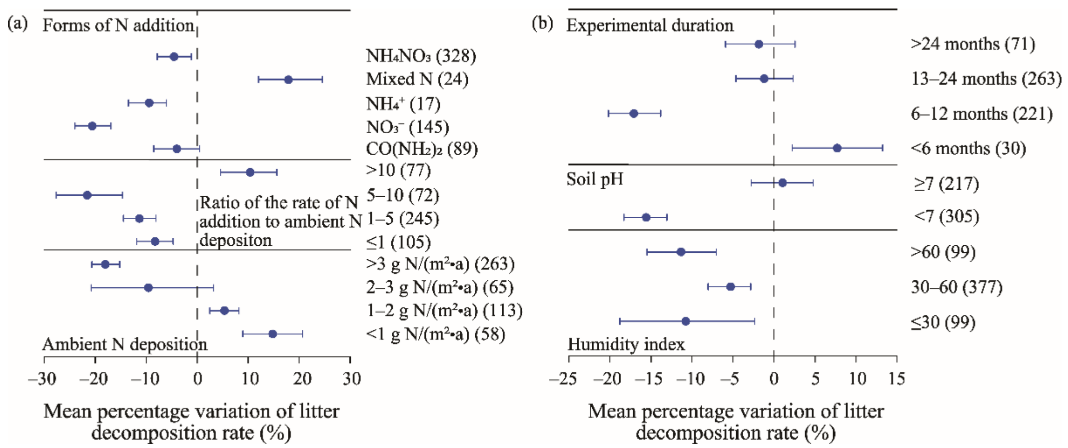

Fig. 3 Mean percentage variation of litter decomposition rate to different forms of N addition, the ratio of the rate of N addition to ambient N deposition, and ambient N deposition (a), as well as mean percentage variation of litter decomposition rate to experimental duration, soil pH, and humidity index (b). Values in the brackets represent the number of observations.

As shown in Figure 4, there were negative relationships of the lnRR of litter decomposition rate with the rate of N addition and ambient N deposition, while a positive relationship was found between the lnRR of litter decomposition rate and the ratio of the rate of N addition to ambient N deposition. The lnRR of litter decomposition rate decreased with increasing MAP, AMT, and HI (Fig. 5). It should also be noted that AMT and MAP had a stronger linear relationship with the lnRR of litter decomposition rate than HI.

Our results indicated that litter quality had a notable effect on litter decomposition rate (Fig. 6). The lnRR of litter decomposition rate was positively correlated with litter C, N, and P content and experimental duration. Conversely, there were negative relationships of the lnRR of litter decomposition rate with litter lignin and cellulose contents. In addition, no significant relationship was observed between the lnRR of litter decomposition rate and either C:N ratio or lignin:N ratio.

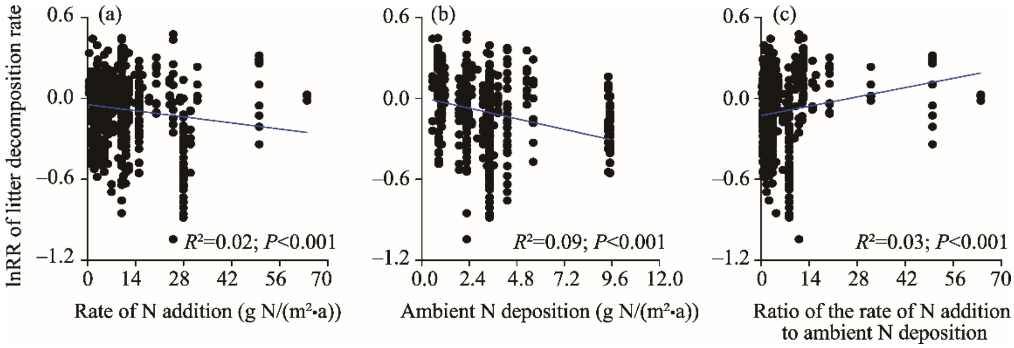

Fig. 4 Linear regression relationships of the logarithmic response ratio (lnRR) of litter decomposition rate with the rate of N addition (a), ambient N deposition (b), and the ratio of the rate of N addition to ambient N deposition (c)

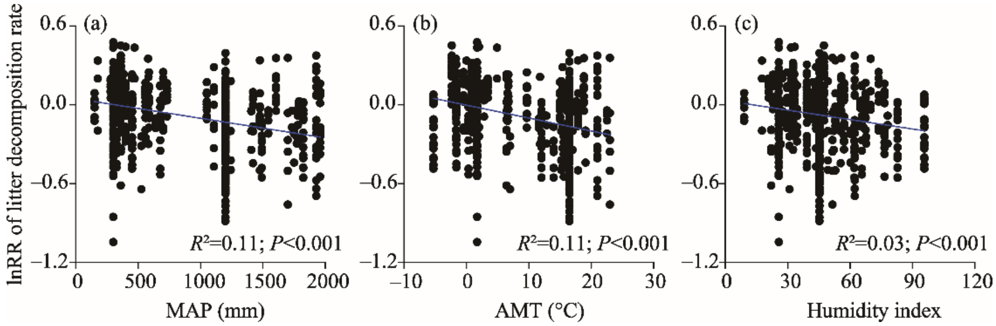

Fig. 5 Linear regression relationships of the lnRR of litter decomposition rate with mean annual precipitation (MAP) (a), annual mean temperature (AMT) (b), and humidity index (c)

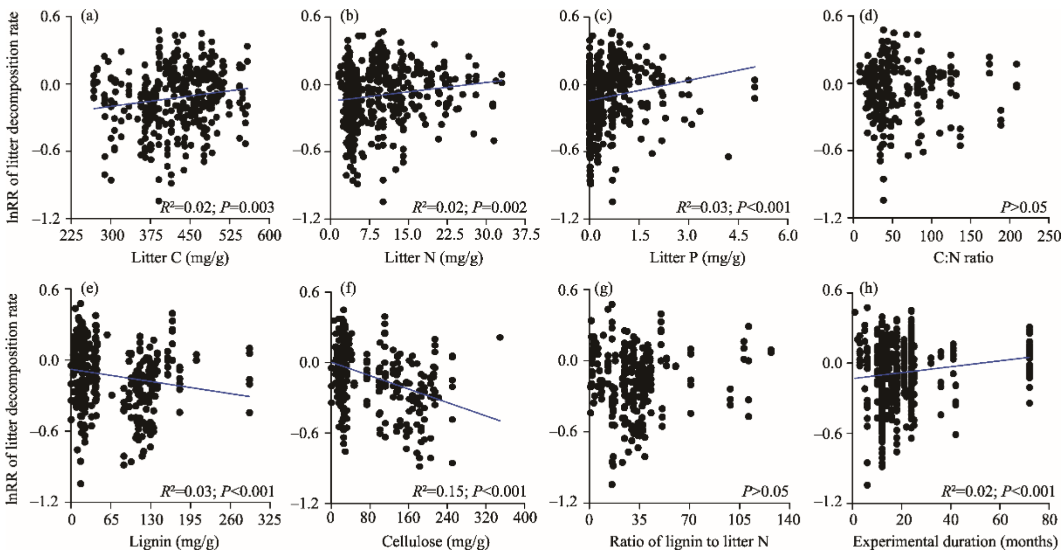

Fig. 6 Linear regression relationships of the lnRR of litter decomposition rate with litter C (a), litter N (b), litter phosphorus (P) (c), C:N ratio (d), lignin (e), cellulose (f), the ratio of lignin to litter N (g), and experimental duration (h)

4 Discussion

4.1 Effects of N addition on litter decomposition rates

A regional-scale meta-analysis of 617 observations from 53 field studies was conducted to investigate how N addition affects litter decomposition rate in terrestrial ecosystems across China. The results indicated that when averaged across the data, N addition significantly inhibits litter decomposition. A previous meta-analysis across terrestrial ecosystems by Zhang et al. (2018) reported that N addition does not significantly change litter decomposition rate, only inducing a small and insignificant inhibitory effect (n=240 observations). Compared with previous meta-analysis studies (Knorr et al., 2005; Zhang et al., 2018), a much larger samples of forest and grassland ecosystems were included in our meta-analysis. This allowed a greater statistical power to identify and compare the effects of N addition on litter decomposition.

In this study, we found that the effects of N addition on litter decomposition rate differs among ecosystems. Owing to the limited availability of data on wetland and cropland ecosystems, we focused on forest and grassland ecosystems in this study. The results indicated that N addition significantly inhibits litter decomposition in forests but promotes it in grasslands. Previous studies have shown substantial variations in the effects of N addition on litter decomposition and have reported positive (Liu et al., 2010; Hou et al., 2020), negative (Liu et al., 2010), and neutral (Hobbie, 2005, 2008) effects. N addition can influence litter decomposition through a number of mechanisms (Hobbie et al., 2012). In recent years, two opposing hypotheses have been suggested to account for the effects of N addition on litter decomposition, seen from the viewpoint of litter quality. The first hypothesis is applicable to N-limited ecosystems, in which microorganisms are more able to degrade lignin to obtain sources of N. The second hypothesis concerns N-saturated ecosystems, where microorganisms can easily obtain N from sources other than lignin (Hobbie, 2008; He et al., 2019).

Enhanced N availability following N addition can significantly decrease soil microbial activity and change the composition of soil microbial community (Treseder, 2008; Hobbie et al., 2012). The negative effects of enhanced soil N on soil microbes can outweigh the positive effects of higher litter quality (increased litter N content and decreased C:N ratio), and finally inhibit litter decomposition (Liu et al., 2010). In forest ecosystems, N addition contributes to soil acidification (Yang et al., 2015) and decreases the soil base cations (K^+, Na^+, Mg^{2+}, and Ca^{2+}). These macronutrients can significantly increase litter decomposition rate (Vivanco and Austin, 2019; Zhou et al., 2020). Furthermore, N addition significantly reduces the activity of lignin-degrading enzymes, thus inhibiting litter decomposition (Hobbie et al., 2012). In contrast, in grassland ecosystems, the degradation of lignin is limited by the availability of soil N. N addition significantly increases the availability of soil N, enhances the concentrations of plant N and P, and decreases plant lignin and cellulose contents. The positive effects of improved litter quality significantly increase litter decomposition rate (Liu et al., 2010; Hou et al., 2020). Although N addition reduces microbial activity and changes the composition of soil microbial community (Liu et al., 2014), the stimulatory effects of improved litter quality exceed the unfavorable influence of increased soil N and promote litter decomposition (Liu et al., 2010).

We found that the rate of N addition exhibits significant and various negative effects on litter decomposition rate in forest ecosystems, ranging from –5.59% to –29.20% with increasing N addition. In grassland ecosystems, litter decomposition rate tends to increase with the rate of N addition, and at a significantly increasing rate with increasing amounts of N addition. This result is inconsistent with the finding of previous reports, that is, at low or high rate of N addition (<7.5 g N/(m^2·a) or >12.5 g N/(m^2·a), respectively), litter decomposition is significantly slowed, while at moderate rates of N addition (7.5–12.5 g N/(m^2·a)), litter decomposition is significantly enhanced (Knorr et al., 2005). Previous meta-analysis studies reported that litter decomposition rate significantly decreases (Zhang et al., 2018) or increases with increasing rates of N addition (Hou et al., 2020). Another study demonstrated that low rate of N addition (<6 g N/(m^2·a)) significantly promotes litter decomposition while moderate (6–12 g N/(m^2·a)) or high (>12 g N/(m^2·a) rate of N

addition profoundly inhibits litter decomposition (Chen et al., 2015). Numerous previous studies have indicated a nonlinear response and threshold to the rate of N addition in terrestrial ecosystems (Bai et al., 2010; Tian et al., 2016; Hou et al., 2020). Our study showed that N addition or ambient N deposition both slow litter decomposition rate, and that the change in litter decomposition rate increases significantly with increasing rates of both N addition and ambient N deposition. Unfortunately, our study was also limited by a paucity of information on the various differences in litter composition, so more field experimental evidence is required to determine whether there is a nonlinear response and threshold for litter decomposition in respect to N addition.

4.2 Factors affecting the effects of N addition on litter decomposition

Previous studies have suggested that litter quality significantly affects litter decomposition and alters ecosystem nutrient cycling (Aerts et al., 2006; Bradford et al., 2014; van Diepen et al., 2015). In our study, increased litter N significantly accelerated litter decomposition. However, increased litter lignin and cellulose contents slowed litter decomposition noticeably. Previous studies have also found that N addition significantly stimulates litter decomposition primarily by improving litter N and decreasing litter lignin and cellulose contents (Liu et al., 2010; Song et al., 2019; Hou et al., 2020). Interestingly, our study also indicated that enhanced litter P content significantly stimulates litter decomposition. To date, the effects of N-induced changes in litter P content on litter decomposition rates remain poorly understood due to insufficient experimental evidence. A study of meadow steppes showed that there is no significant relationship between litter P content and litter decomposition rate (Song et al., 2019). However, another study found that enhanced root P content significantly increases total root decomposition (See et al., 2019). These results suggest that litter P content may have differential effects on the decomposition of above ground litter and that of root litter. In addition, decreased litter lignin and cellulose contents significantly increase litter decomposition, which is consistent with previous observations that N addition noticeably decreases litter lignin and cellulose concentrations, so promoting litter decomposition (Hou et al., 2020).

In our study, the effects of N addition on litter decomposition rate varied greatly according to the forms of N fertilizer addition and the degree of ambient N deposition. NH_4NO_3, NH_4^+, or NO_3^- alone significantly inhibited litter decomposition, while $CO(NH_2)_2$ alone had no effect. However, the addition of mixed forms of N (e.g., a combination of $CO(NH_2)_2$ and glycine) significantly promoted litter decomposition, suggesting that N-based fertilizers could alter the response of litter decomposition to N addition.

Our results that the forms of N addition significantly affect litter decomposition support the previous meta-analysis of Knorr et al. (2005). A study by Zhang et al. (2014) also reported that the type of N addition significantly affects litter decomposition, supporting our results. It is worth noting that all of the data on the use of mixtures of N addition in this study were derived from the study of Dong et al. (2020) on the meadow steppes of Inner Mongolia Autonomous Region, China, involving five grassland species and the litter produced by the entire plant community. Hobbie (2000) reported that mixed N addition in the field experiments significantly promotes the decomposition of *Metrosideros polymorpha* litter. Such studies provide direct evidence that the effects of mixed forms of N addition on litter decomposition rate can differ from those of N fertilization alone, and that the various N fertilizer types can significantly influence litter decomposition rates in different ways. Consequently, global carbon emissions from litter decomposition may be underestimated if based only on results from experiments in which single-source N fertilizers are added (Christopher et al., 2012). Our results highlight the increased effects of mixed forms of N addition on litter decomposition compared with a pure N fertilizer. A study by Dong et al. (2019) indicated that N addition significantly increases litter decomposition, especially when the amounts of inorganic and organic N are equal. These results may explain why soil microbes are not limited by C availability because meadow steppe soils contain vast amounts of stored C. Considering natural atmospheric N deposition, which includes both inorganic and organic N (Zhang and Wang, 2012), we suggest that future research should pay more attention to the effects of mixed-N addition on litter decomposition.

Our results indicate that ambient N deposition significantly promotes litter decomposition to a small degree (5.39%–14.83%) at low rate of N addition (<2 g N/(m^2·a)) and to a high inhibition degree (–18.01%) at high rate of N addition (≥3 g N/(m^2·a)). This may be due to an increase in litter quality at low rate of ambient N deposition, while high rate of ambient N deposition significantly decreases soil microbial activity, changing soil microbial composition, thus resulting in a negative impact on litter decomposition rate (Allison et al., 2009). N addition significantly increases litter decomposition when the rate of N addition is 10-fold greater than the rate of ambient N deposition, but N addition significantly inhibits litter decomposition when the rate of N addition is 10-fold lower than the rate of ambient N deposition. Our results imply that the effects of N addition on litter decomposition are regulated by ambient N deposition and the ratio of the rate of N addition to ambient N deposition. The degree of the effects of N addition on litter decomposition could also be affected by experimental duration, litter quality, soil pH, and HI. Litter decomposition rate is significantly increased over periods of less than 6 months and significantly reduced over a 6–12 months period, while there is no significant effect over a period of more than 13 months. Some previous studies have shown that experimental duration has a significant impact on the effects of N addition on litter decomposition rate, and that litter decomposition rate is promoted during the early stages and inhibited during the latter stages of the experiment (Hobbie et al., 2012; Zhang et al., 2014), indicating that the forms of N addition and experimental duration are important in regulating the process of litter decomposition. Some studies have also found that unstable litter C components rapidly decompose in the early stages owing to the high activity of degrading enzymes, and that litter lignin accumulates during the latter stages due to reductions in lignin-degrading enzyme activity and changes in Gram-negative and Gram-positive bacteria (Zak et al., 2008; Hobbie et al., 2012; Zhang and Wang, 2012), which, to some degree, also explains why N addition accelerates litter decomposition in the early stages of an experiment but slows litter decomposition in the latter stages. Gill et al. (2021) also reported that N addition first accelerates and then slows global leaf litter decomposition, and explained the reasons for this phenomenon in detail.

Our results also suggest that the effects of N addition on litter decomposition rate also varies with soil pH. This may be due to the reduction of litter K^+ and Mg^{2+} in acidic soils compared with neutral or alkaline soils (Mao et al., 2020), which positively correlates with litter decomposition rate (Kaspari et al., 2008; Sardans and Peñuelas, 2015; Vivanco and Austin, 2019). In our study, we found a significant linear correlation between AMT and MAP (P<0.001; Fig. S1). Therefore, we used HI as a climatic index to evaluate the relationship between litter decomposition rate and climatic factors, dividing HI into three groups: 0–30, 30–60, and >60. While HI is an important influencing factor, there are no significant differences among these groups. Linear regression analyses illustrate that the lnRR of litter decomposition rate significantly decreases with increasing MAP and AMT, which is partially consistent with previous meta-analysis studies (Knorr et al., 2005; Zhang et al., 2018). As a result, climate can be a crucial factor regulating the effects of N addition on litter decomposition. Based on the results of N addition field experiments under different conditions in China, we explored the general contribution of N addition to the factors regulating litter decomposition rate. These results are of great significance for the accurate prediction of the effects of global climate change on litter decomposition in the future.

5 Conclusions

The results of our meta-analysis indicate that N addition significantly slows litter decomposition rate across the studies that we examined, while the direction and magnitude of the response are regulated by ambient N deposition, the rate of N addition, the forms of N addition, HI, litter quality, and experimental duration. Further, N addition significantly slows litter decomposition rate in forests and accelerates litter decomposition in grasslands, but litter decomposition exhibits a significantly increasing rate with increasing amounts of N addition. We suggest that in the future, biogeochemical models should consider the differential responses of litter decomposition to different rates of N addition and different ecosystem types to better evaluate ecosystem C cycling under increasing N deposition.

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Appendix

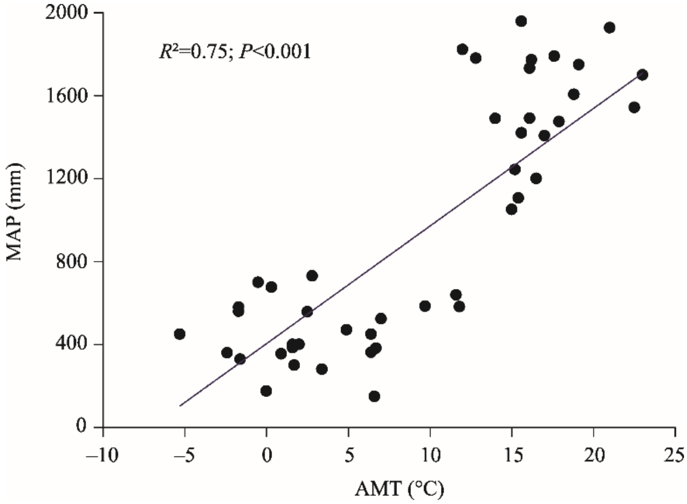

Fig. S1 Linear regression relationship between annual mean temperature (AMT) and mean annual precipitation (MAP) used in the meta-analysis study